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ON INHERITANCE IN EVOLUTION.

BY E. D. COPE.

THE hypothesis of evolution rests on the fact that the character possessed by one generation of animals and plants may be inherited by descendants. In the case of retardation, retrograde metamorphosis, or degeneracy, certain characters are lost by the failure to be inherited. In the case of stationary or persistent type, only the preëxistent characters are inherited. In the case of progressive evolution, characters which are acquired, or added to those already existing, are inherited, thus constituting acceleration.

It is a fact of ordinary observation on animals and men, that many and apparently most of the structural characteristics of one generation are inherited by its offspring. Not only is this the case, but the functioning of organs which depend on minute histological peculiarities is inherited. Such are points of mental and muscular idiosyncrasy; of weakness and strength of all or any of the viscera, and consequent tendencies to disease or vigor of special organs. Darwin has collected in his work on the Descent of Man, numerous instances of the inheritance of various tricks of muscular movement of the face, hands, and other parts of the body.

It is however claimed by Weismann and others, that such characteristics as are thus inherited are not " acquired " but are " congenital." And they appeal to various experiments on the breeding of mutilated animals as evidence of the truth of their position. It is undoubtedly true that mutilations and injuries are not as a general rule inherited. This is also one of the well-known facts of ordinary observation. Were this customary, there would not be at the present time a sound plant or animal on the earth for what individual of either kingdom has not had an ancestor mutilated at some or many periods of past times? But this is a proposition widely different from that which the paleontologist is called on to contemplate.

In the first place, no sharp and fast line can be drawn between "congenital" and "acquired" characters. It has not been shown that the former have not been acquired at an early period, and become by long use incorporated into the organism so as to constitute an essential part of it. It is highly probable that it is just this use which is the index of the value of a character,—which has rendered characters, at first feebly acquired, finally congenital in the fullest sense. The vast majority of mutilations are not useful, and are not generally frequently repeated in the history of a phylogenetic line, so that they are never sufficiently impressed on the organism to become congenital. It is evident that the kind of characters which have become such, are those which result from use in the fullest sense of the word; that is, by countless repetitions continued for immense periods of time. This is clearly the case with respect to the movements of animals which are necessary to their progress through the mediums in which they live; to the obtaining of their food, and to the propagation of their kind. These have been indefinitely repeated, and their mechanical effects on the hard supports of the body, as the skeleton, external and internal, and on the protoplasm whose contractions move the skeleton, were repeated by successive generations before they were inherited, and were by degrees incorporated into the growth-habit of the type, or became, in other words, congenital and inheritable. Such is the hypothesis of inheritance as affecting and effecting progressive evolution; and it is difficult to believe that it is not true. We see much of inheritance about us. The characters which are now inherited have not always existed, and they must have been acquired at some time or another.

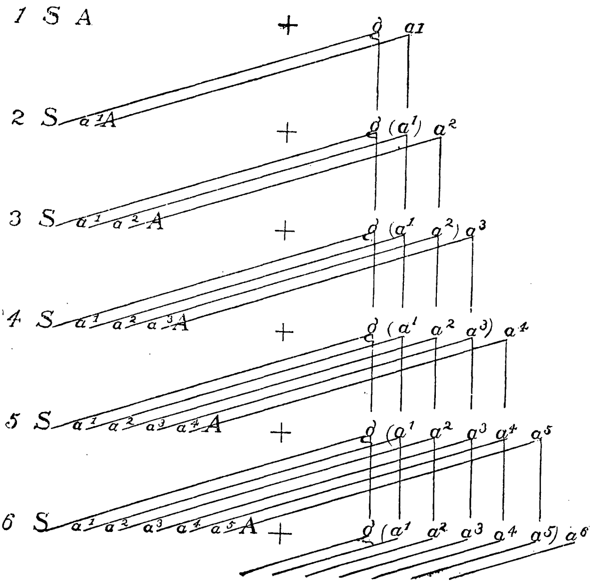
It has been shown by Brooks that bisexual reproduction, by doubling the sources of inheritance, doubles the opportunities for variation of characteristics in descent. This has led Weismann and others to trace all variation to this source. That this proposition is quite insufficient to explain the origin of variation is evident on slight consideration. The appeal to inheritance as a source of variation, no matter whether the inheritance be simple (unisexual) or complex (bisexual) explains nothing. The variations originated at a definite time and in a definite place, whether there be one sex or two, and the presence of the latter merely complicates the question and nothing more. And all characters small or great, whether "sports" or other, have had a definite physical cause.

The basis of the theory that acquired characters are not inherited is as follows: It is asserted by Weismann that the reproductive cells are separated from the primitive layers of the blastoderm at a very early period, and are set apart from those which develop into the other tissues and organs, so as to be uninfluenced by all the later changes undergone by them. In the female they develop into the ovarian cells, and in the male into the mother cells of the spermatozoöids. It is claimed that this isolation is such as to protect them from influences which affect organs and tissues which compose the rest of the body, so that changes which arise in the latter are not transmitted to the former.

Although we may see in the facts adduced by Weismann reasons for the conservatism of type possessed by the reproductive cells, there are various other facts, both of embryology and histology, which restrain us from attaching to the former the importance that the members of his school are accustomed to do. In the first place, since the reproductive cells are derived from the segmentation of the fertilized ovum, they partake of all the characters, whatever they may be, which both parents contribute to the latter, in common with all of the other cells so derived. Now, since the other or "somatic" cells develop the modifications which constitute evolution in their subsequent growth into organs, there is no reason why the reproductive cells which experienced similar influences should not develop similar characters, so soon as they also are prepared to grow into organs. That such influences are experienced by the germ cells is rendered the more probable by the fact that their appearance after segmentation is often not immediate. In some of the rodent mammalia they do not appear until the thirteenth day after the first appearance of the blastoderm. Furthermore the isolation of these cells is not complete after they appear. The continuity of the reticular structure (cytoplasm) of the cells has been repeatedly demonstrated, an arrangement which is essentially connected with their nutrition.

So long as nutrition of the germ-cells continues, the building of structure in which they become the chief agents must be for this reason also subject to the influences which are experienced by all the other cells of the body, under the strains and other stimuli derived from the interaction of the individual and its environment.

The relation of inherited and acquired characters in a series of generations may be graphically represented as follows: Let S represent the aggregate of character of the body (*soma*) of a given species in process of progressive evolution or acceleration. Let


1 S A + g a1
2 S a1 A + g (a1) a2
3 S a1 a2 A + g (a1 a2) a3
4 S a1 a2 a3 A + g (a1 a2 a3) a4
5 S a1 a2 a3 a4 A + g (a1 a2 a3 a4 a5
6 S a1 a2 a3 a4 a5 A + g (a1 a2 a3 a4 a5) a6

g represent the aggregate of characters potential (or dynamically present) in the germ cells of the same individual. For the sake of simplification of the problem I consider here only one sex, and imagine the reproduction to be parthenogenetic. Let A represent the new character acquired by the *soma* under the appropriate stimulus, and let a represent the same characteristic as it is impressed on the germ plasma of the same individual at the same time, and in consequence of the same stimulus. The history of the acquisition and incorporation of newly acquired characters by the line of descent originating with the species $S+g$, may be represented as follows, for successive generations, which are numbered, 1, 2, 3, etc.

Under the appropreate stimulus the soma acquires A and the germ plasma the identical a^1 as the first stage. The character Aa^1 being only inheritable via the germ-plasma, it is represented by a^1 in the second stage or generation, where it appears as an addition to the characters of S and g, so that the soma of the second generation is represented by the expression Sa^1, and the germ plasma by $g\ (a^1)$; (on the supposition that $S\ A + ga^1$ represents the first of a line in which a given character appears). A new character or an additional increment of the same character, appears in the second stage of acceleration "2," and is represented as before, by Aa^2, the A appearing in the soma, and the a^2 being added to the character of the germ-plasma. In the third stage, the new character a^2 appears in the soma, which now becomes Sa^1a^2. The a^2 acquired by the germ-plasma of the second stage, is inherited by that of the third, which is therefore represented by $g(a^1a^2)$. To the third stage is now added the acquisition Aa^3. The a^3 is again incorporated into the soma of the succeeding or former stage, which is therefore represented by the expression $Sa^1a^2a^3$; while the germ-plasma of the same (fourth, "4,") stage, is represented by $g\,(a^1a^2a^3)$, and so on. The lines of immediate inheritance are represented by straight lines. The vertical lines represent the descent of characters from one type of the germ-plasma to a succeeding one; and the oblique lines represent the transmission of the same characters to the soma into which it grows, as the succeeding generation or stage.

The letters a^1, a^2, etc., expressive of characters acquired by the germ-plasma, are numbered for identification only. Should the influences derived from the ancestry of the other sex be added to the diagram its complexity would become inconvenient, and they are therefore omitted. It is to be also observed, that the enumeration of generations as immediately sucessive, as 1-2-3 etc., is to be understood as indicating succession only, and not any exact number of generations.

In the hypothesis of heredity above outlined, it is insisted that the effects of use and disuse are two-fold; viz.: the effect on the soma, and the effect on the germ-plasma. Those who sustain the view that acquired characters are inherited, must, I believe, understand it as thus stated. The character must be potentially acquired by the germ-plasma as well as actually by the soma. Those who insist that acquired characters are not inherited, forget that the character acquired by the soma is identical with that acquired by the germ-plasma, so that the character acquired by the former is inherited, but not directly. It is acquired contemporaneously by the germ-plasma, and inherited from it. There then is truth in the two apparently opposed positions, and they appear to me to be harmonized by the doctrine above laid down, which I call the Theory of Diplogenesis, in allusion to the double destination of the effects of use and disuse in inheritance.

From the preceding considerations we learn that a new character is not inherited unless it is acquired by the germ-plasma, as well as by the soma. Should it fail of the former it will not be inherited, although it may appear in the soma. It is also evident that the same character appears in the soma of later generations by virtue of its inheritance by their germ-plasma. Hence should it fail to appear in the adult soma of one generation, it might arise in a later one; and hence the possibility of atavism, and an alternation of generations. Intermittent stimulus might be followed by intermittent activity of growth energy. This would be especially apt to occur during the assumption of sexuality by animals and plants whose reproduction had been performed by cell-division or budding only. And such is the character of most types of alternate generations; a sexual type alternates with a non-sexual type. The advantages being on the side of sexual reproduction on account of its increased opportunity of variation, it has replaced the more primitive method by the process of natural selection.

The chief source from which acquired characters are introduced into the germ-plasma, and hence into the soma of the next generation, is probably the spermatozoöid; since it is endowed with a greater potential energy than the ovum. The latter furnishes nutritive material for the supply of the needs of growth. That the male is the chief source of variation is also indicated in the numerous cases when he is more active than the female; and hence more under the stimulus of use.

The manner in which influences which have affected the general structure are introduced into the germ cells remains the most difficult problem of biology. For its explanation we have nothing as yet but hypotheses. The one which has seemed to me to be the most reasonable belongs to the field of molecular physics, and it must be long before it is either proved or disproved. I have termed it a "dynamic theory," and it is in some respects similar to that subsequently proposed by Haeckel under the name of the "perigenesis of the plastidule." I have already referred to the phenomena of the building or growth of the added characters which constitute progressive evolution as evidence of the existence of a peculiar species of energy which I termed bathmism. This is to be explained as a mode of motion of the molecules of living protoplasm, by which the latter build tissue at particular points, and do not do so at other points. This action is most easily observed in the beginnings of growth, as in the segmentation of the oösperm, the formation of the blastodermic layers, of the gastrula, of the primitive groove, etc. In the meroblastic embryo the energy is evidently in excess at one part of the oösperm, and in defect at another. This is a simple example of the "location of growth force or bathmism." In all folding or invagination, there is excess of growth at the region which becomes the convex face of the fold; or a location or especial activity of bathmism at that point. All modifications of form can be thus traced to activity of this energy at particular points. A basis is thus laid for a more or less complex organism, and the channels of nutritive pabulum being once established, the location or distribution of the energy is assured in the directions in which they lead. Thus with the establishment of circulating channels nutrition is definitely guided to particular points. It is evident that on this hypothesis the bases of evolutionary change are laid in the embryonic tissues, where indeed bathmism displays its activity in producing the base forms on which all subsequent structure is moulded.

The building energy being thus understood to be a mode of molecular motion, we are not at liberty to suppose that its existence is dependent on the dimensions of the organic body which exhibits it. It is as characteristic of the organic unit or plastidule as the mode of motion which builds the crystal is of the simplest molecular aggregate from which the crystal arises. Bathmism has however no other resemblance to crystalloid cohesion. The latter is a simple energy which acts within geometrically related spaces, without regard to anything else but the present compulsion of superior weight energy. In bathmism we see the resultant of innumerable antecedent influences, which builds an organism constructed for adaptations to the varied and irregularly occurring contingencies which characterize the life of living beings. As this resultant is distinctive for every species, Bathmism must be regarded as a generic term, and the characteristic growth-energy of each species as distinct species of energy, which presents also diversities expressive of the peculiarities of individuals. If the doctrine of kinetogenesis be true, this energy has been been moulded by the interaction of the living being and its environment. It is the expression of the habitual movements of the organism which have become impressed on the reproductive elements. It is evident that these and the other organic units of which the organism is composed possess a memory which determines their destiny in the building of the embryo. This is indicated by the recapitulation of the phylogenetic history of its ancestors displayed in embryonic growth. This memory has perhaps the same molecular basis as the conscious memory, but for reasons unknown to us, consciousness does not preside over its activities. The energy which follows its guidance has become automatic, and it builds what it builds with the same regardlessness of immediate surroundings as that which is displayed by the crystallific growth energy. It is incapable of a new design. Consciousness is necessary for the origin of a design, since design cannot come into being without sensation and conscious memory. Hence we are lead to suppose that the designed handiwork displayed by bathmism had its origin in conscious states, and under the influence of the effort of the organism to adapt itself to its environment, internal and external. Not only does the conclusion seem reasonable, but it is supported by the well-known effects of mental states on various functions of the adult organism; such as the formation of ptomaines in the digestive tract, the depression and acceleration of the heart's action, the control of erectile tissues, etc.; to say nothing of ordinary muscular movements.

It is for such reasons that I have maintained that there would have been no evolution of animal types at least, if acquired characters were not inherited. Promiscuous variations there would have been, but it is certain that the probabilities are enormously against the persistence of any of them beyond one generation, should they not be inherited. That any succession of such variations could be profitable is also highly improbable, to say nothing of the improbability of their displaying the direct relation to use which we find in them in point of fact. The explanation of the appearance of such continued series of direct adaptations, such as has been demonstrated for instance in the phylogeny of the horse, is only explicable to my mind on the supposition of the inheritance of the direct effects of use, which use has been primarily directed by sensation. Without these factors evolution would have been suppressed at its inception, just as we see that it has been retrogressive or downward so soon as one or another of these factors has been withdrawn.

The time when the impressions of physical habits are conveyed to the reproductive elements has an important bearing on the question of inheritance. The life of an animal may be divided into three periods; those of embryonic life, of adolescence, and of maturity. During embryonic life impressions are exclusively somatic, and can be only obtained through or from parental stimulus and parental environment. Such will reach the embryo though nutrition, and through the direct mechanical contacts and strains of the environment. The environment of the oviparous forms is external to the parent; that of viviparous forms is the walls of the oviduct, uterus, etc., within the parent. Ryder has shown with much reason that the nature of the contact of the chorion with the walls of the oviducts or uterus has determined the shape of the placenta; and that the invagination of the embryo which resulted in the development of the amnion is a result of gravitation. While these facts have an important bearing on inheritance, they have but a collateral relation to evolution; since the embryo, whether in utero or in ovo, has little opportunity of experiencing the external influences which are only possible at later periods of life. It is during adolescence that the normal activities of maturity except reproduction, are first practiced, whether inherited or learned for the first time. The superior capacity of the adolescent stage for acquisition in all directions is well-known, and it is reasonable to suppose that since growth is not completed, changes in its details can be most readily introduced. It is to this period of life then that we must look for the effective influence of the factors of evolution in the acquisition of new characters of the soma. And if the nervous, muscular and other tissues react at this period most readily to external stimmuli, it is to be supposed that the developing reproductive cells possess the same characteristic, and record in their molecular movements the influences which are experienced by the entire body. Such influences on the reproductive cells, repeated millions of times from generation to generation, must produce a definite effect on them, in spite of the conservatism which their comparative isolation imposes on them. It is difficult to see how it can be otherwise in view of the evident mechanical origin of the characters which have succeeded each other as the steps of the evolution of vegetable and animal types.

The transmission of acquired characters is evidently principally accomplished during the adult period. While the influence on the soma is greatest during adolescence, the influence on the germ-plasma is greatest during maturity. Here habits formed during adolescence are practiced with especial energy and frequency. The influence on the constantly renewed germ-plasma is correspondingly greater, and transmission is of course more certain. Some characters seem to have been mainly acquired during maturity. Such is the permanent dentition of the higher Mammalia, which does not appear until or after maturity. In this case the influence of use on the germ-plasma must be more energetic than that on the soma. It is however not unlikely that the fundamental characters of mammalian dentition were laid during adolescence, since in the primitive types the temporary dentition was nearly wanting. The tritubercular molar was established at that time, and owes its present existence to inheritance. Only the sectorial and lophodont types have been added since the extensive development of the milk dentition in geologic time.

The preceding statements do not of course constitute an explanation of the exact manner in which a stimulus which effects say the contraction of a muscle, effects molecular movements of the nuclei of the reproductive cells. This is a question of organic molecular physics; a science which has made scarcely a beginning. That the transmission of such influence is primarily through the nervous system and secondarily through nutrition, may be safely assumed. That the modus operandi is similar to that which produces reflexes may be also reasonably supposed. How the records of these movements become reflexes, is concentrated in a reproductive cell, is a question to be solved only in a more advanced stage of knowledge of organic physics than we now possess.

Speculation in this direction takes the following forms. The energy or molecular movement must be transmitted to the germplasma through a material or molecular basis. This basis, it may be supposed, must be that which receives the mechanical impression which is to produce a corresponding modification of growth energy in the ovum or spermatozoöid; that is, in the case of a modified bone articulation, particles of matter must pass from the latter through the medium of the circulation to the reproductive cells. The alternative hypothesis is, that the nervous energy (neurism) which directs the active region to make or omit to make a given movement, the result of which is to be structural modification in the young, is impressed through nervous channels, on the germ-cells of either sex. In this case the transmission of particles of matter is not necessary, as material connection through the nervous threads already exists.

To the first of these points of view belong the pangenesis theory of Darwin, and the modified pangenesis of Brooks.[1] These

[1] The Law of Heredity, Baltimore, 1883, p. 80.

hypotheses present the difficulty that we must conceive of each particle or "gemmule" derived from a given part of the organism finding its way through the circulation to its exact place in the growing embryo; or otherwise, of transmitting its peculiar mode of motion to the correct molecules of the embryo, without error as to locality. The difficulties to be encountered in accomplishing such a feat seem to be insuperable. The transmission of a mode of motion organized in a central nervous system, is less inconceivable. This central system is the seat of a composition of incoming stimuli and of outgoing energies, the resultant of both combined constituting the active agency in the production of automatic adaptive or intelligent adaptive movements of any and all of the organs. It appears to me that we can more readily conceive of the transmission of a resultant form of energy of this kind to the germ-plasma than of material particles or gemmules. Such a theory is sustained by the known cases of the influence of maternal impressions on the growing fœtus. Going into greater detail we may compare the building of the embryo to the unfolding of a record or memory, which is stored in the central nervous organism of the parent, and impressed in greater or less part on the germ-plasma in the order in which it was stored. The basis of memory is reasonably supposed to be a molecular (or atomic) arrangement from which can issue only a definite corresponding mode of motion. That such an arrangement exists in the central nervous organism is demonstrated by automatic and reflex movements. That the entire record is not repeated in automatic and reflex acts, but only that part of it which was last acquired, may be regarded as due to the muscular and other systems concerned in it having performed it most recently, and having for a longer or shorter period omitted to perform the older movement, because the latest structures of the organs would render the performance of the old movements impossible. In other words, the physiological division of labor extends to memory at the basis. In the case of the germ-plasma no specialisation exists, so that the entire record may be repeated stage after stage, thus producing the succession of type-structures which embryology has made familiar to us. In the process of embryonic growth, one mode of motion would generate its successor in obedience to the molecular structural record first laid down in the ovum and spermatozoöid, and then combined and recomposed on the union of the two in the oöspore, or fertilized ovum.

Were all cells identical in characters, everyone would retain the structural record, or memory of its past physical history, as do the unicellular organisms. Evolution has however so modified most of the structural units of the organic body that none but the nervous and reproductive cells retain this record, in greater or less perfection. And the nervous cells have been specialized as the recipients of new impressions, and the excitors of definite corresponding movements in the cells of the remainder of the organism. The somatic cells retain only the record or memory of their special function. On the other hand, the reproductive cells, which most nearly resemble the independent unicellular organisms, retain first the impressions received during their primitive unicellular ancestral condition; and second, those which they have acquired through the organism of which they have been and are only a part. And the principal medium through which they can receive such impression is that system of cells called the nervous system, which has been specialized through use and natural selection to receive impressions from without, and to transmit them to such parts of the organism as are capable of receiving them. And the only other cells which can retain and record the entire record are the reproductive cells.

This is the logical result of the considerations which have occupied the preceding pages, and is the carrying out of the Bathmism theory of heredity, of which I have given hitherto only the bare outline.

Since Darwin, successive contributions have been made to the theory of heredity in its relation to evolution. In 1878 and 1871 the present writer advanced the dynamic hypothesis, but made no attempt to explain the mode of conveyance of dynamic impressions and modifications to the germ-cells. The theory of "perigenesis" proposed by Haeckel in 1873 is of the same character, and is deficient in the same way. The modified pangenesis theory of Brooks, published in 1883, attempts to supply the defect found in the previous conceptions, but does so by assuming with Darwin the intermediation of gemmules, a hypothesis to which objection has been made in the preceding pages. Brooks's theory also fails to admit the origin of variations through mechanical stresses, although he seeks for the origin of gemmules through the lack of equilibrium between the organization and its environment, which embraces that proposition in a less precise form. To Weismann we are indebted for the exposition of the separate origin and relative isolation of the germ-plasma, but no explanation of the origin and inheritance of new characters is offered. Ryder[2] has especially dwelt on the physiological division of labor seen in the tissues of the organism, and on the special function of the germ-plasma as the recipient of impressions through the processes of metabolism; but he does not go into greater detail.

ON VARIATION: WITH SPECIAL REFERENCE TO CERTAIN PALÆOZOIC GENERA.

BY PROF. JOSEPH F. JAMES.

THE question, "What are the limits of a species?" has been discussed for over two hundred years, and a satisfactory reply to it has not yet appeared. None of the numerous answers seem to meet all requirements. The conception of what a species really is has, too, been greatly modified since the publication of the "Origin of Species" by Darwin. It has been assumed by some of the more radical naturalists that species as entities are very rare, and that their boundaries are so indefinite that practically few exist. It is true that certain forms of animals and plants are distinct, or possess so few relatives that they seem to stand isolated. The Venus's Fly-trap among plants, and the Duck-bill among animals, seem to occupy positions which cut them off from all other plants or animals; but such cases are certainly exceptional. On the other hand, there are whole groups of

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[2] AMERICAN NATURALIST, 1890, p. 85.